RECORDINGS OF HIGH WING-STROKE AND THORACIC VIBRATION FREQUENCY IN SOME MIDGES

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The highest known wing-stroke frequencies of insects have been recorded in male specimens of the dipterous families Chironomidae and Ceratopogonidae (Heleidae), where values of 1000/sec. have been obtained (Sotavalta, 1947). These recordings were made by registering acoustically the pitch of the flight-tone emitted by these insects during free flight. Until now, very few recordings of high wing-stroke frequencies have been obtained by the aid of other methods. Boettiger and Furshpan (1952) have obtained a wing-stroke frequency of 500/sec. in a chironomid midge, using electrostatic methods combined with cathode-ray oscillograph.

That still higher values of wing-stroke frequency can be produced, at least under artificial conditions, appears from the experiments reported below. The frequency determinations were made by three methods. The pitch of the flight-tone in free flight was determined acoustically; the flight-tone in free flight was also recorded by means of a microphone and high fidelity tape recorder, and with an accurate frequency check of 1000/sec. from a beat-frequency oscillator, transposed to recording film by means of a double-beam cathode-ray oscillograph; the thoracic vibration during fixed flight was registered by means of a piezo-electrical crystal pick-up and similarly recorded on tape and film. Male specimens of a small green species of *Chironomus* (s.lat.) and of a tiny species of *Forcipomyia* (Ceratopogonidae) were used in the experiments.

Experiments on Chironomus: Flight-Tone and Thoracic Vibration Frequencies

In order to record the flight-tone in free flight, the specimen was allowed to fly unmounted in a small glass chamber attached to the front of the microphone. The insect was stimulated to flight by letting it respond phototactically to a bright lamp near the glass chamber, or by shaking the glass chamber. The maximum duration of flight in the chamber obtained in this way was about 7–8 seconds. The flight-tone frequency recorded was about 600–650/sec. (Fig. 1), with occasional higher and lower values. Acoustical determinations were made before the experiment by allowing the insect to fly in a test-tube, the mouth of which was pressed against the ear. The general range of the flight-tone was determined as $d^2\sharp$–e^2 (622–659/sec.), and thus thoroughly agreed with the oscillographic recordings.

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The thoracic vibrations were recorded in other specimens by mounting the insect on a stylus inserted in a crystal pickup (Roeder, 1951). Releasing the flight reflex by removing a platform from under the tarsi induced fixed flights for as long as 15 seconds, which could be recorded.

The thoracic vibration frequency was found to be about 520–580/sec. (Fig. 2a). A loudspeaker was turned on during the experiments, and it emitted a loud tone which thus was produced not by the wings but by the *thorax*. The frequency of

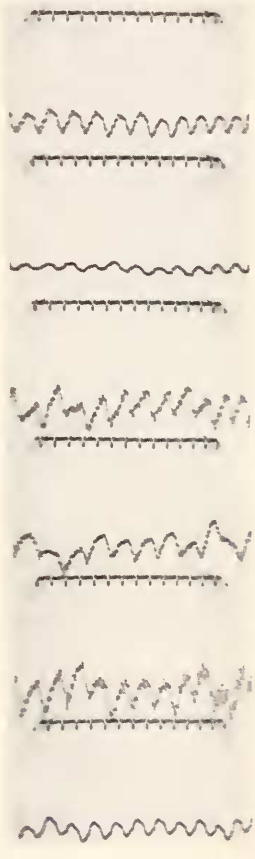

FIGURE 1. Flight-tone of *Chironomus* sp. and time-check 1000/sec. Frequency 600–680/sec.

this tone was determined acoustically as 554–587/sec. At the same time also the flight-tone produced by the wings was checked acoustically, and it was found in this case to have a pitch of c^2✻–d^2 (554–587/sec.), thus identical with the other determinations above.

The wings were then mutilated with transverse cuts, and a recording taken after each cut. First the left wing was cut to about half of its length. The thoracic vibration frequency (Fig. 2b), the frequency of the loudspeaker tone and of the flight-tone were again found to agree completely, being about 650–700/sec. (e^2–f^2).

The right wing was then cut to the equal half-length, and the frequency rose to about 830–880/sec. ($g^{2}\sharp$–a^{2}) (Fig. 2c). Both wings were then cut close to their bases, and the increased frequency was found to be about 1300–1400/sec. (e^{3}–f^{3}) (Fig. 2d).

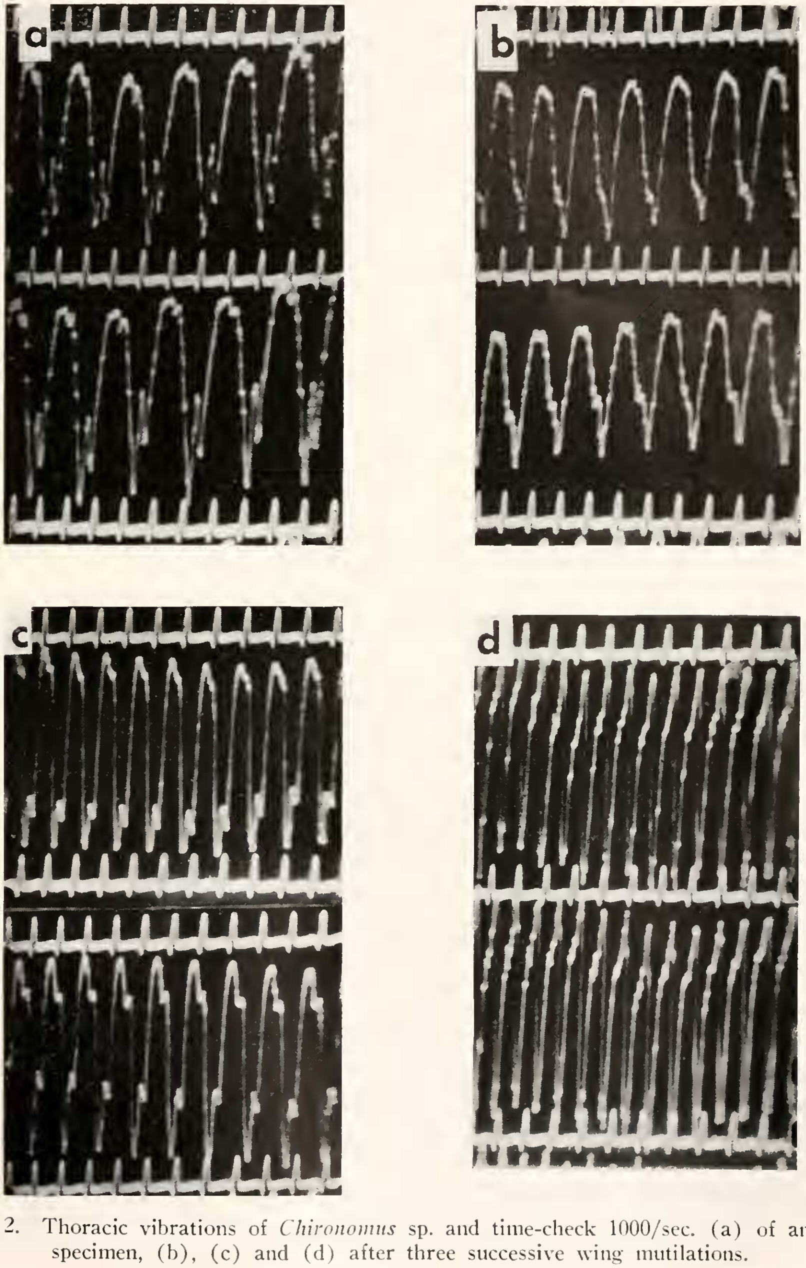

FIGURE 2. Thoracic vibrations of *Chironomus* sp. and time-check 1000/sec. (a) of an intact specimen, (b), (c) and (d) after three successive wing mutilations.

Experiments on Forcipomyia: Flight-Tone Frequencies

The specimen was allowed to fly unmounted in a glass chamber attached at the front of the microphone and flight was induced as in *Chironomus*. Also the flight-tone was checked acoustically before the experiment as above. The flight-tone frequency was found to be about 800–950/sec. ($g^2\sharp$–$b^2\flat$) (Fig. 3), and a complete agreement between the oscillographic and acoustic recordings was observed.

Unfortunately, it was not possible to mount a specimen of this species on the stylus, because even a slight heating of the mounting wax either killed the insect or, as it seemed, paralyzed the thoracic muscles. Any glue used for mounting did not adhere to the smooth and shiny surface of the thorax. Therefore no recording of the thoracic vibrations of these insects was possible.

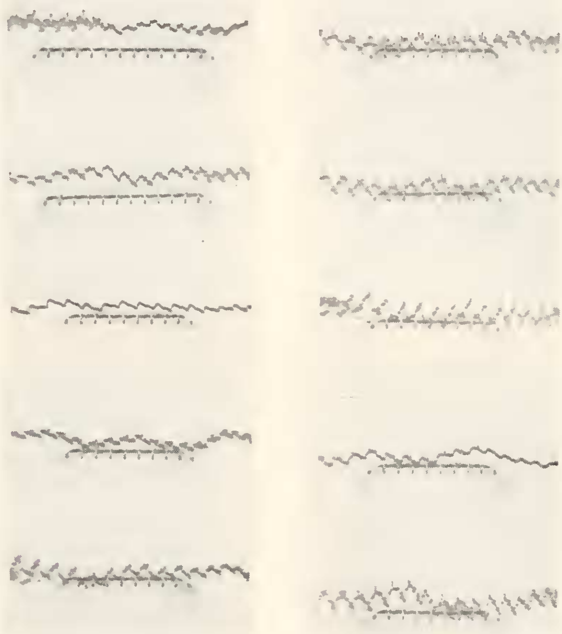

Figure 3. Flight-tone of *Forcipomyia* sp. and time-check 1000/sec. Frequency 800–950/sec.

Wing-mutilation experiments in this species were carried out with unmounted specimens. Since cutting the still more minute wings of such minute insects even with iridectomy scissors was extremely difficult without damaging the insect otherwise, only one experiment was successful. The wings were removed close to the base and the tone emitted determined acoustically by allowing the insect to "fly" in a small test-tube in front of an electric lamp. The flight-tone, which in the intact insect was $g^2\sharp$–a^2 (831–880/sec.), rose to f^3–$f^3\sharp$ (1397–1480/sec.). After this the test-tube with the midge was placed in an incubator at 37° C. for about 20–30 seconds. When it was taken out, the flight-tone was immediately determined. It proved to be a^3–$c^4\sharp$ (1760–2218/sec.). The midge, unfortunately, died so quickly after this experiment that no tape or film recording of these high frequencies was possible.

Discussion

In order to produce a wing-stroke frequency of 1000/sec. the indirect flight muscles have to perform their complete cycle of contraction and relaxation in one msec. If the frequency is 2200/sec., this time is 0.45 msec., and thus both sets of indirect flight muscles perform 2200 contractions and relaxations during one second. Though it certainly is very doubtful whether there exist in nature insects which in an intact state possess a wing-stroke frequency comparable to the latter value, the producing of it artifically shows that the flight muscles are *capable* of such extreme performances under appropriate conditions. This fact also provokes a question about the minimum limit of time interval after which a muscle in general is able to repeat its contraction. Since the contraction frequency must be correlated with the intrinsic speed of the muscle, *i.e.,* with the ratio of contraction speed at zero load to fiber length (Hill, 1949), it follows that this limit, in turn, is correlated with the minimum limit of size in animals having well developed muscular organization. The problem whether motor nerves can transmit separate impulses with such a frequency is excluded because the indirect flight muscles of Diptera and of certain other insect orders possess a unique ability to maintain a rhythm of contractions without a motor nerve impulse preceding each contraction, as shown by Pringle (1949) and Roeder (1951). No microscopical insects, in the proper sense of the word, are known; therefore it is evident that in approaching this size limit the limit of contraction frequency also is approached. Since the speed of contraction also depends on load, even the most minute known insects cannot have an extremely high frequency of wing-strokes unless also the *relative* size of their wings is very small.

Since the energy output of a large and of a small insect is proportional to the cube of their linear dimensions, while the energy requirement is proportional to the fifth power of their linear dimensions, this leaves a margin in small insects within which the wing-stroke frequency can be increased (Sotavalta, 1952). Therefore a minute size is a *conditio sine qua non* for an extremely high wing-stroke frequency. In spite of this, however, there most likely appear additional factors which have a relatively greater significance as energy consumers in small than in large insects. The effect of drag in propulsion (*cf.* Sotavalta, 1952) and the dissipation of heat from the body to the air are proportional to the surface and therefore may necessitate a higher energy consumption in a small insect than predicted by the above reasoning.

Summary

1. Experiments on recording flight-tones and thoracic vibrations in intact and wing-mutilated midges (*Chironomus, Forcipomyia*), using double-beam cathode-ray oscillograph and film and acoustic method, are reported.

2. In *Forcipomyia,* a wing-stroke frequency of 2218/sec. was the maximum value recorded, produced in a specimen with wings cut and exposed to high temperature.

3. Some aspects of the occurrence of such high frequencies in insects, correlated to the muscle contraction frequency in general, and of the energy consumption in small insects are discussed.

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